# A Reassessment of Sinornis santensis and Cathayornis yandica (Aves: Enantiornithes)

JINGMAI O'CONNOR\*1 AND GARETH DYKE2

<sup>1</sup> Dinosaur Institute, Natural History Museum of Los Angeles, 900 Exposition Boulevard, Los Angeles, CA 90007, United States of America, and University of Southern California, 3651 Trousdale Parkway ZHS 117, Los Angeles, CA 90089, United States of America

<sup>2</sup> School of Biology and Environmental Science, University College Dublin, Belfield Dublin 4, Ireland jingmai@usc.edu · gareth.dyke@ucd.ie

ABSTRACT. The taxonomy of the first two enantiornithine birds named from the Early Cretaceous of China, *Cathayornis yandica* and *Sinornis santensis*, has remained controversial despite the relative completeness of both holotype specimens. This is because *C. yandica* is regarded as a junior synonym of *S. santensis* by some researchers, and as a distinct taxon by others. This question is revisited in this paper; in order to determine the validity of *C. yandica*, we conduct a detailed morphological review of both holotype specimens. Despite proposed synonymy we argue that there are clear and distinct anatomical differences between the two taxa; indeed our morphological observations demonstrate that the two birds constitute valid and distinct branches in the diverse enantiornithine evolutionary radiation. Of course, and like many other groups of fossil vertebrates, the diverse Cretaceous bird lineage Enantiornithes requires taxonomic revision yet in the case of *C. yandica* and *S. santensis* we attribute much of the confusion to: (1) incomplete specimens being designated as holotypes, and (2) the absence of clear morphological character-based taxon diagnoses founded on rigorous anatomical comparisons.

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Enantiornithes are the most diverse known lineage of Mesozoic birds (Chiappe, 2002; Chiappe & Dyke, 2007; Dyke & Nudds, 2009) with over 60 species named, and in China dozens, if not hundreds, of undescribed specimens (O'Connor, 2009). However, despite this apparent diversity, the taxonomy of Enantiornithes remains largely unreviewed and at least a third of named species are based upon extremely fragmentary, sometimes non-overlapping, fossil material (Table 1) (for example, six named species from the Cretaceous of Uzbekistan are based on coracoid fragments; Panteleyev, 1998) (see O'Connor, 2009). While revisions have been limited, several taxa have nevertheless been

questioned and re-evaluated: Nanantius valifanovi has been synonymized under Gobipteryx minuta (Chiappe et al., 2001); Cathayornis yandica under Sinornis santensis (Sereno et al., 2002); Liaoxiornis delicatus and Lingyuanornis parvus have been considered Euenantiornithes indeterminant (Chiappe et al., 2007); and Aberratiodontus gui has been synonymized under Yanornis martini (Zhou et al., 2008a). Of these revisions to the taxonomy of Enantiornithes, most have passed largely unquestioned into subsequent literature with the exception of the proposed synonymy of Cathayornis yandica and Sinornis santensis, in which there is no consensus (cf. Li et al., 2006; Chiappe et al., 2007; Cau

& Arduini, 2008). In this paper we provide a review of this issue and a detailed morphological study which supports the validity of *C. yandica* as a separate taxon from *S. santensis*.

Unnamed or unpublished material is referred to by collection number with the institutional prefix. Relevant institutional acronyms are BNHM (Beijing Natural History Museum, Beijing), IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing), DNHM (Dalian Natural History Museum, Dalian), CAGS (Chinese Academy of Geological Sciences, Beijing), GMV (Geological Museum of China, Beijing), LP (Institut d'Estudis Illerdencs, Lleida, Spain).

## **Background**

In recent years the extremely rapid rate of new discoveries of fossil birds from China has resulted in publications presenting strikingly similar taxa sometimes appearing almost simultaneously (e.g., Zhou et al., 1992; Sereno & Rao, 1992; see also Hou & Chen, 1999; Ji & Ji, 1999; Zhou & Zhang. 2001; Gong et al., 2004), as was the case with the descriptions of Sinornis santensis (Beijing Natural History Museum, Beijing; BNHM BPV 538a,b) [Sereno & Rao, 1992] and Cathayornis yandica (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; IVPP V9769a,b) [Zhou et al., 1992], the first two enantiornithine birds described from China (Sereno & Rao, 1992, Sereno et al., 2002, Zhou et al., 1992). Owing to the rapid rate of discovery and publication, detailed comparisons of Chinese fossil birds have often been absent and thus diagnostic distinctions between 'species' have often been left unclear or are later proven to be unverifiable from the original publications (i.e., through photographs and figures) (e.g., Hou, 1997; Zhang et al., 2006; Li et al., 2006; Gong et al., 2008). This was certainly the case in the original publications of S. santensis (Sereno & Rao, 1992) and C. yandica (Zhou et al., 1992).

In a publication a decade after it was first named, *C. yandica* was synonymized under *S. santensis* by Sereno *et al.* (2002), while in the same volume an argument was made for the validity of the former (*C. yandica*; Zhou & Hou, 2002). Synonymy was not strongly supported (or refuted) empirically in either chapter and as a result *C. yandica* and *S. santensis* are still treated as distinct taxa by some (Li *et al.*, 2006; Chiappe *et al.*, 2006) and as synonyms by others (Chiappe *et al.*, 2007; Cau & Arduini, 2008).

The situation has been further complicated by the subsequent referral of additional species to the genus *Cathayornis*: *C. caudatus* [Hou, 1997], *C. aberransis* [Hou *et al.*, 2002], and *C. chabuensis* [Li *et al.*, 2008]. Given that the validity of *C. yandica* is uncertain, the assignment of new specimens and/or species to *Cathayornis* first needs to be justified with morphological support for the validity of the original genus (as independent from *Sinornis*). This then needs to be followed by morphological support for a close relationship between the new specimen and the holotype of *C. yandica*, as well as identifying distinguishing features that indicate the specimen is a new species. The issue of the proposed synonymy with *Sinornis* has not been discussed, and thus these species require re-evaluation.

In Enantiornithes, diagnosing a new species or justifying higher-level relationships can be particularly difficult. Enantiornithine birds are usually small and morphologically uniform—like their extant perching passerine counterparts. Without very detailed inspection, small morphological differences may go unobserved and multiple 'real' species

may be regarded under one taxon (e.g., Martin & Zhou, 1997; Zhou, 2002). Alternatively, without good preservation and preparation of these small specimens, it is difficult to separate true morphologies from those that may be diagenetic or taphonomic (e.g., flattening, crushing, bending). Currently, despite the known diversity of enantiornithines (Table 1), the inter-relationships of taxa and evolutionary trajectories within the clade remain poorly understood (but see O'Connor, 2009). Resolution is required within enantiornithine taxonomy so that studies of enantiornithine biology, phylogenetics and lineage dynamics can proceed (Chiappe & Walker, 2002; Chiappe *et al.*, 2007; Dyke & Nudds, 2009; O'Connor, 2009).

The holotype specimens of S. santensis and C. yandica are both small fossil birds, comparable to one another in size and with a similar mode of preservation in which the bones are preserved as voids in a slab and counterslab (Figs 1, 2). Because their bones are not preserved, moulds and casts have been made from the specimens to facilitate their study; these casts are much more informative than the original slabs. Both the slab and counterslab of the C. yandica holotype were studied from the original and the cast (IVPP V9769a,b), the main slab of S. santensis was studied from a cast (BNHM BPV 538a,b), and both slabs were studied from original photographs. Both holotype specimens were collected in the northwest of Liaoning Province, northeastern China near Chaoyang City. The holotype of *C. yandica* was collected from the Xidagou locality, just south of Boluochi, while S. santensis was discovered just west of Shengli (Hou, 1997; Zhou & Hou, 2002).

However, although the specimens are similar in preservation, the discernable information that can be gained from each differs greatly (Figs 1,2). While the holotype of C. yandica (IVPP V9769a,b) is largely disarticulated and incomplete (Fig. 1), that of S. santensis is preserved in articulation but is also missing some elements (BNHM BPV 538a,b) (Fig. 2). The two specimens almost exactly mirror each other in terms of wellpreserved skeletal elements: the holotype of C. yandica (IVPP V9769a,b) includes a fairly well-preserved skull and pectoral girdle but its pelvic girdle and hindlimbs are incomplete and disarticulated, while the holotype of S. santensis (BNHM BPV 538a,b) preserves an articulated pelvic girdle and hindlimbs but has a poorly preserved partial skull and pectoral girdle. Thus, characters used to distinguish S. santensis (note that a diagnosis is absent from the original publication; Sereno & Rao, 1992) are difficult to assess in C. yandica (e.g., the presence of a blade-like ischium in C. yandica; Sereno & Rao, 1992) and vice versa (e.g., the presence of notches in the sternum of S. santensis; Zhou et al., 1992).

The original publications on S. santensis and C. yandica did not directly compare the two specimens (Sereno et al., 2002). The first paper (Sereno & Rao, 1992) on S. santensis also lacked a formal diagnosis and thus there were no clear morphologies to compare with other known taxa at the time (Sereno & Rao, 1992). Later a proper diagnosis was provided for the taxon (Sereno et al., 2002) but all the morphologies cited have since been recognized as general synapomorphies of enantiornithines or more exclusive clades within such as Euenantiornithes (Chiappe & Walker, 2002; O'Connor, 2009), with the possible exception of the 'scimitar-shaped' ischium (Sereno et al., 2002). In contrast, the original publication on C. yandica (Zhou et al., 1992) provided a very thorough diagnosis, however most of the characters cited in this description, although rare features at the time, are now known to have a wide distribution throughout Aves (e.g.,

Table 1. Published records of enantiornithine birds listed chronologically. Abbreviations: AUS, Australia; EUR, Europe; N-AM, North America; S-AM, South America.

Cincinna	ma (		Illatoriui	UIIIUIIIII	3	) cur	matchiai
Gobipteryx minuta	Asia 15	1974	partial skull and mandible	Enantiornithes indet.	AUS	1999	proximal tibiotarsus
Alexornis antecedens	N-AM 15	9261	leg/wing bones	Enantiornithes indet.	AUS	1999	distal tibiotarsus
Gobipteryx minuta	Asia 15	9261	partial skull and mandible	Enantiornithes indet.	AUS	1999	distal tibiotarsus
Enantiornis leali	S-AM 19	1861	isolated coracoid, scapula and humerus	Eoenantiornis buhleri	Asia	1999	complete w/ feathers in single slab
Gobipteryx minuta	EUR 15	1981	two partial skeletons, bone fragments	Gurilynia nessovi	Asia	1999	humerus fragments and a partial coracoid
Kizylkumavis cretacea	Asia 15	1984	partial humerus	Hebeiornis fengningensis	Asia	1999	nearly complete specimen in slab
Zhyraornis kashkarovi	Asia 15	1984	partial synsacrum	Liaoxiornis delicatus	Asia	1999	complete in slab
Zhyraornis logunovi	Asia 15	1984	partial synsacrum	Lingyuanornis parvus	Asia	1999	complete in counterslab
Avisaurus archibaldi	7	1985	tarsometatarsus	Cathayornis aberransis	Asia	2000	partial skeleton in slab
Nanantius eos		9861	tibiotarsus	Protopteryx fengningensis	Asia		two nearly complete specimens
Noguerornis gonzalezi		6861	partial skeleton	Euenantiornithes indet.	EUR		pellet
Sazavis prisca	Asia 15	6861	partial tibiotarsus	Gobipteryx minuta	Asia	2001	partial skull
Cathyaornis yandica		1992	nearly complete in slab and counterslab	Longipteryx chaoyangensis	Asia		two nearly complete specimens
Concornis lacustris		1992	postcranial skeleton in single slab	Avisaurus archibaldi	N-AM		distal metatarsal III
Neuquenornis volans	S-AM 19	1992	partial skeleton	Enantiornithes indet.	EUR	2002	tibiotarsus
Sinornis santensis		1992	nearly complete in slab	Enantiornithes indet.	Asia	2002	right humerus, incomplete
Enantiornis martini		1993	partial coracoid	Enantiornithes indet.	S-AM	2002	partial right half of a mandible
Enantiornis walkeri		1993	partial coracoid	Eocathayornis walkeri	Asia	2002	proximal skeleton in slab and counterslab
Lectavis bretincola	Į	1993	isolated tibiotarsus and tarsometatarsus	Halimornis thompsoni	N-AM		scapula, humerus, femur and pygostyle
Otogornis genghisi		1993	wing in slab	Iberomesornis romerali	EUR		two partial skeletons
Soroavisaurus australis		1993	two tarsometatarsi	Longirostravis hani	EUR	2003	nearly complete in single slab
Yungavolucris brevipedalis		1993	five isolated tarsometatarsi	Aberratiodontus wui	Asia	2004	nearly complete in slab and counterslab
Avisaurus gloriae	V	1995	tarsometatarsus	Vescornis hebeiensis	Asia	2004	nearly complete in single slab
Boluochia zhengi		1995	partial skeleton in slab	Enantiornithes indet.	Asia	2005	isolated wing in single slab
Eoalulavis hoyasi		9661	partial skeleton in single slab	Dalingheornis liwei	Asia	2006	nearly complete in slab
Euenantiornithes indet.	В	1996	isolated bone fragments	Dapingfangornis sentisorhinus	Asia	2006	nearly complete in single slab
Lenesornis maltshevskyi		9661	partial synsacrum	Elsornis keni	Asia	2006	partial skeleton
Nanantius valifanovi		1996	partial skeleton	Enantiornithes indet.	Asia	2006	isolated wing in single slab
Avisaurus n.sp.	7	1997	partial skeleton	Enantiornithes indet.	Asia	2006	partial pelvis and hindlimbs
Cathayornis caudatus		1997		Euenantiornithes indet.	Asia	2007	nearly complete in slab
Cuspirostrisornis houi		1997		Euenantiornithes indet.	Asia	2007	nearly complete in slab
Euenantiornithes indet.	_	166	proximal skeleton in slab	Martinavis cruzyensis	EUR	2007	humerus
Largirostrornis sexdentornis		1997	nearly complete in slab	Martinavis sp.	S-AM		four humeral fragments
Longchengornis sanyanensis		1997	partial skeleton in slab	Martinavis vincei	S-AM		complete humerus
Longirostrisornis		1997	partial skeleton in slab	Martinavis vincei	S-AM	2007	distal humerus
Abavornis bonaparti		8661	partial coracoid	Paraprotopteryx gracilis	Asia	2007	nearly complete slab and counterslab
Abavornis sp.		8661	partial coracoid	Alethoalaornis agitornis	Asia	2008	five nearly complete slab specimens
Alexornithiformes indet.		8661	partial coracoid	Cathayornis chabuensis	Asia	2008	partial skeleton in slab and counterslab
Catenoleimus anachoretus		8661	partial coracoid	Enantiophoenix electrophyla	EUR	2008	partial skeleton w/ feathers
Enantiornithes indet.		8661	partial femur and coracoid	Enantiornithes indet.	EUR	2008	femur
Explorornis nessovi		8661	partial coracoid	Enantiornithes indet.	EUR		tarsometatarsus
Explorornis sp.		1998	partial coracoid	Pengornis houi	Asia		nearly complete in single slab
Explorornis sp.		8661	partial coracoid	Rapaxavis pani	Asia		complete in single slab
Incolornis martini		1998	partial coracoid	Shanweiniao cooperorum	Asia		nearly complete in slab and counterslab
Incolornis silvae	Asia 15	1998	partial coracoid	DNHM D2950/1	Asia	2010	nearly complete in slab and counterslab

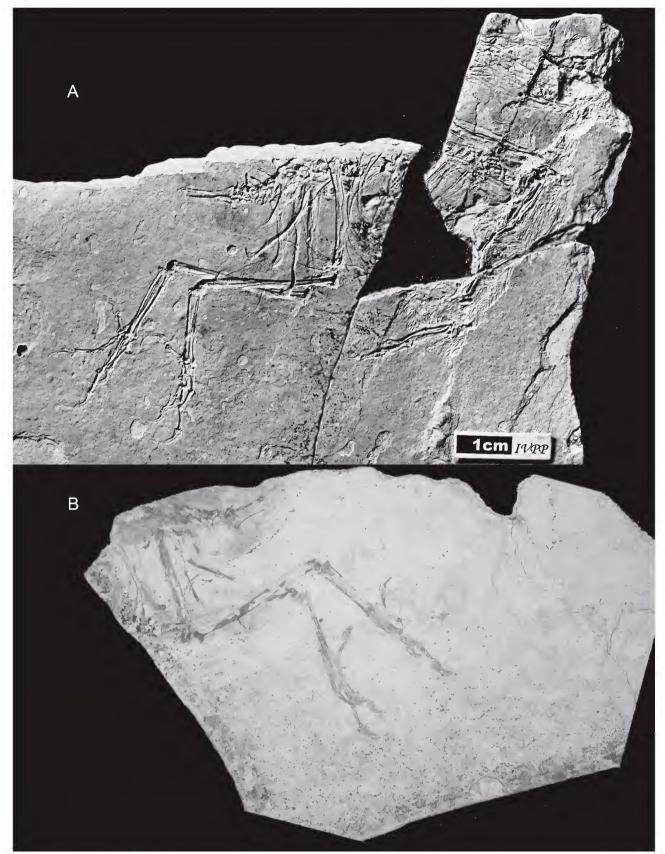


Figure 1. Photograph of the slab and counterslab of *Sinornis santensis*: (A), BNHM BPV 538a; and (B), BNHM BPV 538b. Scale bar equals 10 mm. Photographs from Zhou Zhonghe (A) and Luis Chiappe (B).

strut-like coracoid, low keel on sternum, straight scapula, toothed premaxilla and dentary, clawed manus; Zhou *et al.*, 1992; O'Connor, 2009; O'Connor *et al.*, 2009). Following the

subsequent deluge of Chinese fossil discoveries, an updated diagnosis that distinguishes the specimen from other taxa was provided (Zhou & Hou, 2002).

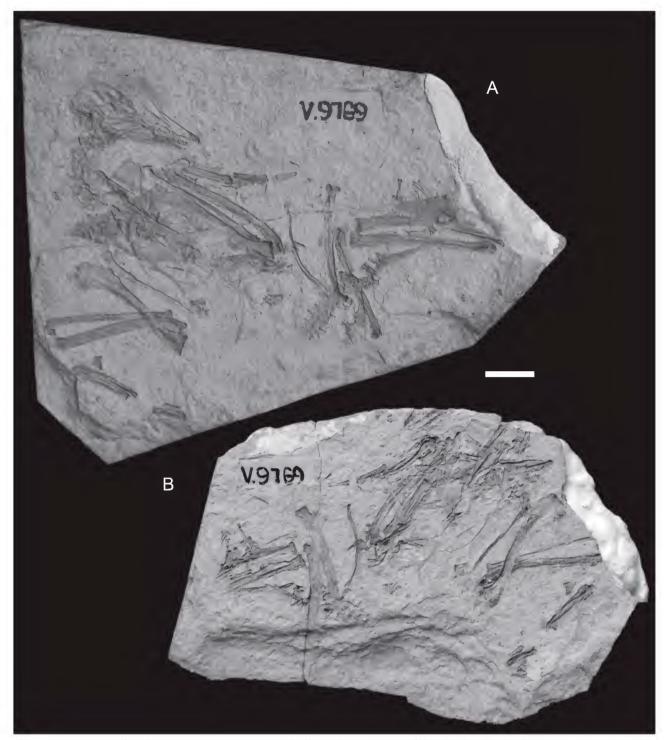


Figure 2. Photograph of Cathayornis yandica: (A) IVPP V9769a; and (B) IVPP V9769b. Scale bar equals 10 mm.

Arguments for the synonymy of the two taxa are based on morphology (Sereno *et al.*, 2002). Despite having identified differences between the two holotype specimens, including differences in size, proportions of the manual claws, and the morphology of the minor digit, Sereno *et al.* (2002) nevertheless used similarities in preserved pygostyle and ischium morphology as primary arguments for the synonymy of the two species. Zhou & Hou (2002) also discussed the issue of synonymy and provided clear diagnoses for both species which included morphological differences, some of which were also recognized by Sereno *et al.* (2002). Zhou & Hou (2002) also argued that the locality difference alone

may be enough to justify separating the two taxa.

## Cathayornis yandica vs. Sinornis santensis

**Locality**. The holotype specimens of *S. santensis* and *C. yandica* were described from different localities in the Early Cretaceous Jiufotang Formation (upper Jehol Group: 120 Ma; Zhou, 2006), approximately 10 km apart, with Chaoyang City as the closest major geographic indicator (Sereno *et al.*, 2002; Zhou & Hou, 2002; Zhou & Zhang, 2006). Although this has been used to distinguish the two taxa, differentiation based on inferred geological age, or geographical separation, makes assumptions about a

species range or success. Among extant birds there are many examples of species that have huge geographical ranges, thus such assumptions are for obvious reasons inherently weak. The error associated with dating sediments is typically large and limiting an extinct taxon based on knowledge of an extant analogue bears no validity other than a proposed possibility. Comparisons with geographical ranges of similar (e.g., diet, ecology, size, etc) modern taxa or average species duration through time may be used as valid arguments for erecting a new taxon, however, such arguments should be made only when they can be justified and well supported by cited data. In the case of *S. santensis* and *C. yandica*, no detailed justification has been provided.

**Morphology**. All the morphological variation that has been previously used to either support the existence of two species, or the synonymization of *C. yandica* under *S. santensis*, is reviewed here. Some previously published data are questioned and alternative interpretations of the preserved features are provided. Note that, although a size difference of approximately 10% is present between the two holotype specimens (Sereno *et al.*, 2002; Zhou & Hou, 2002), because the ontogenetic stage of each specimen is unknown (this aspect of enantiornithine biology also remains unclear) this difference should not be considered diagnostic until further explored through histological analysis. Furthermore, this size differential falls well within the typical size range for a comparably-sized species of living bird (Dunning, 1993).

**Skull**. Despite the very poor preservation of the skull in the S. santensis holotype, from which little or no information can actually be gained (Figs 1, 3B), Sereno et al. (2002) compared the morphology of the nasals and maxilla of the two specimens (Fig. 3). Both were described as possessing broad nasals which expand caudal to the external nares and have a triangular caudal margin (Sereno et al., 2002). We concur that the nasal of the holotype of C. yandica is wellpreserved; the nasals articulate medially for approximately half their length, separated rostrally by the nasal (frontal) processes of the premaxilla and caudally by the frontals (Fig. 3A). The rostrally directed maxillary and premaxillary processes are sharply tapered; of these, the maxillary process is fairly short, although contributing to the lateral border of the external nares (in contrast with taxa in which this process is absent and the nasal contribution to the external nares is restricted to the caudal and dorsal margins, e.g., DNHM D2950/1, Rapaxavis pani and Longipteryx chaoyangensis; Zhang et al., 2000; Morschhauser et al., 2009; Wang et al., 2010). In S. santensis, however, no nasal can be definitively identified because the skull is comprised of numerous incomplete bone fragments, none of which preserve any morphology that allows unequivocal identification. Even if Sereno & Rao (1992) are correct and some bone fragments that are in articulation with what has been interpreted as the frontal (Sereno & Rao, 1992) are indeed nasals (Fig. 3B), with only the caudal half of this region preserved we cannot determine if they were expanded (relative to the rostral half).

The caudal half of the maxilla of *S. santensis* was described as differing from that of *Archaeopteryx* because its dorsal and ventral margins are parallel and the jugal ramus does not taper significantly caudally (Sereno *et al.*, 2002). These details are impossible to verify, however, because neither holotype specimen, *S. santensis* or *C. yandica*, has a maxilla that clearly preserves this region (Fig. 3). The left maxilla in the *C. yandica* holotype is visible nearly in articulation with the premaxilla; the premaxillary and

jugal rami appear subequal (as opposed to the elongate premaxillary ramus in longipterygids; O'Connor et al., 2009). The maxilla of C. yandica has a long and thin caudodorsally directed nasal process; the caudal articulation with the jugal is not completely preserved so we cannot rule out that the jugal ramus was tapered, although, in its preserved portions, this ramus does have parallel rostral and dorsal margins. In S. santensis, the maxilla is even less clear; one element may represent the maxilla based on the presence of what appears to be a nasal process, as in C. vandica (absent in Gobipteryx minuta; Chiappe et al., 2001) (Fig. 3B). If correct, the premaxillary ramus is not preserved; the dorsal and ventral margins of the jugal ramus are parallel except for the distalmost articulation with the jugal where this process tapers abruptly (as opposed to the slow tapering of this process in Archaeopteryx; Elzanowski, 2002), morphologically similar to Hebeiornis fengningensis (= Vescornis hebeiensis; Xu et al., 1999; Zhang et al., 2004). We conclude that, given the skull preservation in the holotype of S. santensis, no cranial morphologies are useful for either distinguishing, or aligning, the two taxa.

**Vertebral column**. While on the one hand we agree with Sereno *et al.* (2002) that the thoracic vertebral morphology preserved in the holotypes of *S. santensis* and *C. yandica* are comparable, this region of the skeleton is generally conserved among Early Cretaceous enantiornithines (Chiappe & Walker, 2002) and neither specimen preserves any deviant morphologies (O'Connor, 2009). Note however that while Sereno *et al.* (2002) recorded the number of sacral vertebrae as eight in *S. santensis*, it is impossible to count in this region of the skeleton because the articulated pelvic girdle is preserved in lateral view, obscuring the sacrals from view (Fig. 1).

The pygostyles of *S. santensis* and *C. yandica*, as noted by Sereno *et al.* (2002), are also morphologically very similar, with dorsal and ventral processes that reach beyond the articular facet and ventrolaterally directed processes that rapidly diminish distally, causing a marked taper (Sereno *et al.*, 2002; Zhou & Hou, 2002) (Fig. 4). Since the discovery of these specimens, however, several new species have been described that possess the same morphology, now regarded as typical of most enantiornithines (Zhang *et al.*, 2000; Chiappe & Walker, 2002; Chiappe *et al.*, 2002; Li *et al.*, 2006; O'Connor, 2009). As noted by Zhou & Hou (2002), the pygostyles of the two taxa do differ in length with respect to their overall body size, which can only be considered a true morphological difference and thus a diagnostic character: the pygostyle of *C. yandica* is nearly 25% longer than that of *S. santensis* (Fig. 4).

Thoracic limb. Zhou & Hou (2002) listed differences in the morphology of the ulnare as a diagnostic distinction between the two taxa: the ulnare of *C. yandica* is described as having a larger metacarpal incision than that of *S. santensis* (Zhou & Hou, 2002). The ulnares certainly differ in morphology between the two specimens (Fig. 5); the ulnare in the holotype specimen of *S. santensis* (Fig. 5B) is much more U-shaped, with a deeper and narrower incision relative to that of *C. yandica*, which is much shallower and wide (*sensu* Zhou & Hou, 2002). The fairly deep incisure preserved in the *S. santensis* holotype was noted by Sereno & Rao (1992) and compared to the ulnare morphology of more derived birds such as *Ichthyornis*. The narrow and deep metacarpal incisure on the ulnare of *S. santensis* differentiates this taxon from *C. yandica*.

The morphology of the manus is also similar in both species (Fig. 5): *S. santensis* and *C. yandica* have small claws

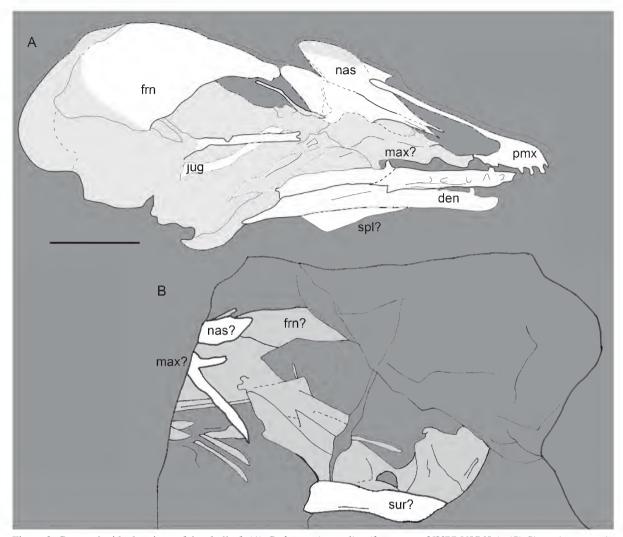


Figure 3. Camera lucida drawings of the skull of: (A) Cathayornis yandica (from cast of IVPP V9769a); (B) Sinornis santensis (from cast of BNHM BPV 538a). Abbreviations: den, dentary; frn, frontal; jug, jugal; max, maxilla; pmx, premaxilla; spl, splenial; sur, surangular. Question marks denote equivocal determinations.

on both their alular and major digits and have short alular digits that do not distally surpass the distal end of the major metacarpal. The proximal carpometacarpus was considered to be unfused in S. santensis as opposed to fused in C. yandica (Sereno & Rao, 1992; Zhou et al., 1992), however this character is unclear and cannot be unambiguously determined in either taxon owing to preservation (Fig. 5). The absence of an intermetacarpal space in the holotype of C. yandica has also been used to distinguish the two taxa but this morphological difference was dismissed as diagenetic by Sereno et al. (2002). After reviewing the morphology preserved in IVPP V9769, we concur with the latter interpretation. The preserved morphology is very distinctive and observed among other enantiornithines (e.g., Rapaxavis, Dapingfangornis sentisorhinus, Hebeiornis), with the minor metacarpal having a rectangular crosssection, dorsoventrally wider than craniocaudally thick. In fully articulated enantiornithines, the cranial surface of the minor metacarpal is concave so that the size of the intermetacarpal space does not appear the same from dorsal and ventral views. While no space appears present in either carpometacarpus in dorsal view (IVPP V9769a), a small space is clearly visible in ventral view (IVPP V9769b; Fig. 5A). As in other enantiornithines, the minor metacarpal is proximally contiguous with the pisiform process (IVPP

V9769b), slightly wrapping around the major metacarpal distally (e.g., *Eoenantiornis buhleri*, *Hebeiornis*, *Rapaxavis*; Hou *et al.*, 1999). This morphology is also present in the holotype of *S. santensis* (Fig. 5B). The intermetacarpal space still appears larger in *S. santensis* however this may be due



Figure 4. Pygostyle of (A) Cathayornis yandica (IVPP V9769a); (B) Sinornis santensis (cast of BNHM BPV 538a). Scale true for A and B.

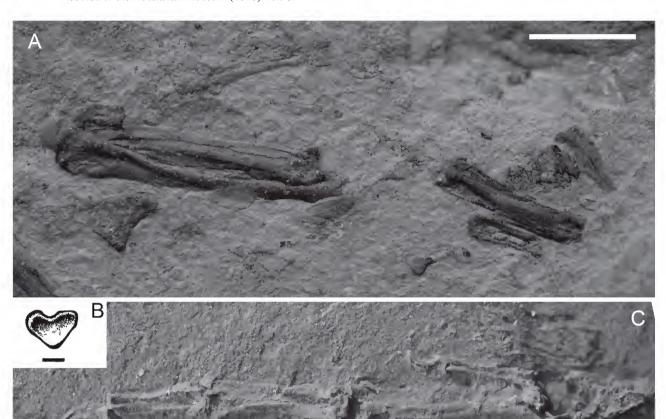


Figure 5. Carpometacarpus of (A), Cathayornis yandica (IVPP V9769b, left manus); and (B), Sinornis santensis (cast of BNHM BPV 538a, right manus). Scale bars equal 5 mm.

to the better preservation of the manus (in articulation) in the holotype specimen (Fig. 5B).

Sereno et al. (2002) also noted a difference in the relative proportions of the manual claws between the holotypes of S. santensis and C. vandica, with the major ungual larger than the alular ungual in the former taxon and the two claws subequal in the latter. Zhou & Hou (2002) considered that the alular claw is larger than the major claw in C. yandica, with claws of subequal size in S. santensis. These different interpretations based on the same specimens result partially from the poor preservation of the manus in C. yandica and the very small difference in size that is being considered here. Based on our observations, the manual claws are nearly subequal in both taxa, although the major claw is proportionately larger in S. santensis while the alular claw is larger in C. yandica (Fig. 5). The two specimens therefore preserve the opposite condition, and this morphological difference, although slight, can be used to distinguish the two taxa.

The morphology of the first phalanx of the minor digit also differs between the taxa. In the holotype of *C. yandica* this phalanx is clearly straight, rectangular to trapezoidal, tapering distally (Fig. 5A) while in *S. santensis* it is curved with a concave ventral margin (Fig. 5B) (Zhou & Hou, 2002). The curved phalanx of *S. santensis* is also proportionately longer than that of the hand of *C. yandica* (Zhou & Hou, 2002). The morphological disparity of this phalanx between the two specimens was noted by Sereno *et al.* (2002) but was

dismissed as intraspecific variability. The curvature present in the *S. santensis* holotype is clearly distinct from the straight morphology preserved in the *C. yandica* holotype. Given the differences already noted between the specimens, however, additional specimens of *S. santensis* are required to argue that this curvature is indeed intraspecific variation. Until then, this morphology is considered diagnostic of *S. santensis*.

Pelvic girdle. The pelvic girdle is well-preserved in the holotype of S. santensis, nearly complete, fully articulated and missing only the preacetabular wing of the ilium (Fig. 6A). This contrasts with the almost completely disarticulated and incomplete pelvic girdle of the holotype of C. yandica. Although both specimens were reported by Sereno et al. (2002) to have ischia of similar morphology, this cannot be verified given the poor preservation of this region in the holotype of C. yandica. This element was reconstructed by Zhou & Hou (2002); however this information comes from a referred specimen first published by Hou (1997—no collection number). The specimen is an isolated fully articulated pelvis; Zhou & Hou (2002, fig. 7.7H) illustrated the pubis as bent in lateral view, a morphology that cannot be confirmed in C. yandica IVPP V9769. With insufficient justification for the assignment of this pelvis to C. yandica, information from this specimen is not utilized here pending further investigation.

The ischium of *S. santensis* is consistent with that of other enantiornithines in that it possesses a large proximally located dorsal process but lacks an obturator process (Chiappe &

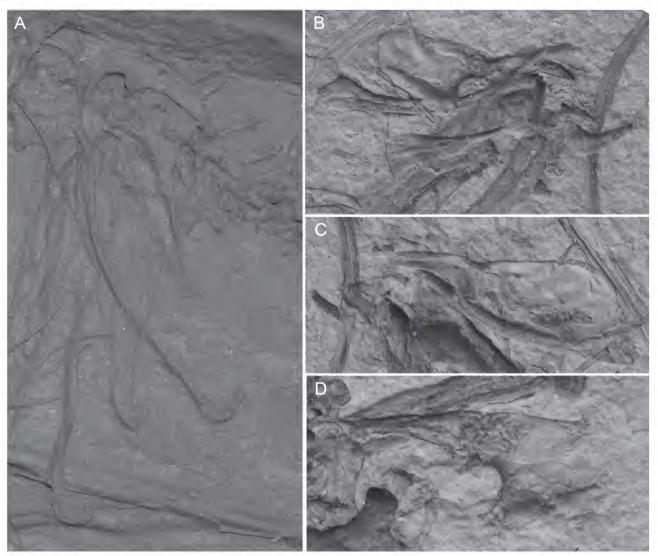


Figure 6. (A), cast of the pelvic girdle in Sinornis santensis BNHM BPV 538a; (B), left ilium of Cathayornis yandica IVPP V9769b; (C), left ilium IVPP V9769a; (D), right ilium IVPP V9769a.

Walker, 2002). The dorsal curvature of the caudal ischium present in the holotype specimen of *S. santensis* is also present in *Eoenantiornis* and clearly distinct from the straplike ischia present in some other Early Cretaceous Chinese enantiornithines (e.g., *Longipteryx*, DNHM D2950/1). Visible in the cast of the IVPP V9769b is what appears to be the corpus of the ischium preserved overlapping the ilium. While detailed morphologies remain unclear, this bone shows the same dorsal and medial curvature that is present in the *S. santensis* holotype (contra Sereno & Rao, 1992). Given the poor preservation of the ischium in the holotype of *C. yandica*, this morphology is subject to interpretation and cannot be used to align the two species; medial curvature of the ischia is also known in several other enantiornithines (e.g., *Concornis lacustris*, *Dapingfangornis*, *Rapaxavis*; Sanz & Buscalioni, 1992).

Cathayornis yandica was described as lacking an antitrochanter on its pelvis while this structure is reportedly present in S. santensis (Zhou & Hou, 2002). This difference is also very difficult to determine because of the lack of fusion and complete disarticulation of the pelvic girdle in the holotype of C. yandica and the absence of a well-preserved ischium in this specimen; however, because the antitrochanter is typically located just where the ischium and ilium contact, the presence of an antitrochanter cannot

be ruled out. A small triangular antitrochanter is clearly present in the holotype of *S. santensis*; the structure is located primarily on the ilium, consistent with other Early Cretaceous enantiornithines (e.g., CAGS-IG-05–CM-06; JOC pers. obs.). This region of the ilium is only visible on the left in the holotype of *C. yandica*, but damaged so that no antitrochanter appears present.

Zhou & Hou (2002) also diagnosed *C. yandica* as having a rim over the craniodorsal margin of the acetabulum; this feature is clearly visible on the holotype of *S. santensis* extending over the entire cranial and dorsal margins of the acetabulum, contiguous with the antitrochanter (Fig. 6A). In *C. yandica* this rim can only be seen on the craniodorsal margin and is cut off where the ilium is damaged so that it cannot be determined if the crest continued and was also contiguous with an antitrochanter, as in *S. santensis*. A supracetabular process (the 'dorsal antitrochanter' of Sereno *et al.*, 2002) is also present in both specimens (Fig. 6A,B,C).

Although the ilium in both species is very similar in terms of its general shape and proportions, close comparison of the two specimens reveals additional minor differences in the morphology of the postacetabular wing (Fig. 6). The dorsal margin of this wing of the ilium in *S. santensis* is dorsally convex while the ventral margin is slightly concave so that the

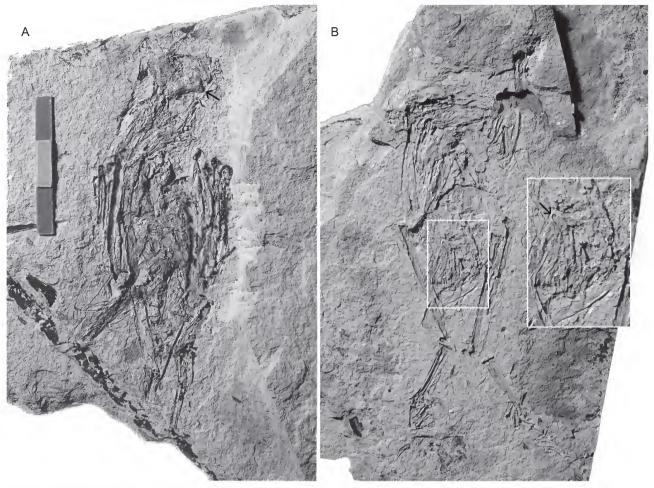


Figure 7. Holotype of (A), Cathayornis aberransis, IVPP V12353; and (B), Cathayornis caudatus, IVPP V10917. Scale bar is true for both specimens and totals 30 mm.

entire postacetabular wing is slightly curved in a caudoventral direction (Fig. 6A). The postacetabular blade is thus strongly triangular. In contrast, the left postacetabular process of *C. yandica* has a straight dorsal margin with a ventrally concave ventral margin and is directed caudally (Fig. 6C,D). The process tapers caudally in both specimens but much less in the *C. yandica* holotype, which terminates in a blunt distal margin. In the holotype of *S. santensis* this termination forms a sharper point (Fig. 6A). Overall, the morphology of *C. yandica* is more strap-like than that of *S. santensis* (Fig. 6D).

A three-dimensionally preserved enantiornithine (CAGS-IG-05–CM-06) from the slightly younger Xiagou Formation, Gansu, China, possesses a nearly complete and fully articulated pelvic girdle, and displays the same straight morphology as *C. yandica* (JOC pers. obs.). This results in a difference in the shape of the 'ilioschiadic fenestra' between *S. santensis* and the Xiagou enantiornithine, which suggests that the morphology observed in *C. yandica* is not a preservational artifact but a true difference that can be used to differentiate the two taxa.

## Differentiating S. santensis and C. yandica

After examining the morphologies proposed to either align, or separate, the two specimens, we find significant morphological variation between the two holotypes that we feel justifies maintaining the two as distinct taxa. Preserved characters have been identified, and are supported here, that can be used to formulate a rigorous differential taxonomic

diagnosis for the first time.

Sinornis santensis (BNHM BPV 538) differs from *C. yandica* (IVPP V9769) in that: (1) the first phalanx of the minor digit is curved (cf. straight in *C. yandica*) and proportionately longer relative to the first phalanx of the major digit; (2) the claw of the major digit is proportionately larger relative to that of the alular digit; (3) the postacetabular wing of the ilium is proximally broad, curved and tapered distally (cf. 'strap-like' in *C. yandica*); (4) the ulnare is U-shaped with a relatively deep narrow incisure (wide and shallow incisure in *C. yandica*) and; (5) the pygostyle is shorter (3/4 the length of that of *C. yandica*).

Referred specimens of Cathayornis yandica. A number of specimens have been referred to C. yandica both in publications and informally in small museums around China (Martin & Zhou, 1997; Hou, 1997; Hou et al., 2002; Zhou & Hou, 2002; JOC, pers. obs.). Indeed, many of these specimens preserve regions of the skeleton poorly known in the holotype, such as an articulated pelvic girdle (Hou, 1997, fig. 54, p. 136, no collection number) and hindlimbs (IVPP V9936, Zhou & Hou, 2002; IVPP V10533, V10904, Hou, 1997) that offer the possibility of further comparison with S. santensis and additional morphological differentiation if correctly assigned. For example, both C. yandica and S. santensis have a plantarly excavated tarsometatarsus formed by keel-like medioplantar and lateroplantar margins of metatarsals II and IV respectively, a morphology observed in a number of enantiornithines (e.g., avisaurids). Although the distal ends of the metatarsals in C.

yandica are not preserved in the holotype specimen, a well preserved referred specimen IVPP V9936 reveals that the metatarsals of these birds are arranged in a single horizontal plane while the trochlea of metatarsals II and IV of *S. santensis* (visible in the holotype specimen) are displaced plantarly. However, because the morphological information comes from an unconfirmed referred specimen, this cannot yet be considered a true diagnostic character of *C. yandica*. The small overall size and subtly of the morphological differences between these birds suggest that only a complete and detailed inspection of all referred specimens will determine their taxonomic assignment. Pending such a revisionary study, it is recommended that referred specimens should not be used to supplement data from the holotype or used with extreme caution.

Cathayornis aberransis, C. caudatus and C. chabuensis. Although we have presented an argument in favor of the validity of C. yandica, this alone does not completely clarify the taxonomic status of the genus. Three other species have to date been assigned to Cathayornis; the validity of two species is variably accepted, while the third has only recently been described (C. chabuensis-Li et al., 2008). Although C. caudatus and C. aberransis have been considered invalid by some (Sereno et al., 2002; Zhou & Zhang, 2006), the only published record of this was not corroborated by morphological evidence (Zhou et al., 2008b). These two taxa, and three others (Longchengornis sanyanensis, Cuspirostrisornis houi, and Largirostrornis sexdentornis; Hou, 1997) have been synonymized under C. yandica based on the fact the holotype specimens of these taxa were all collected from the same locality, despite the presence of morphologies distinct from C. yandica in some specimens (e.g., Longchengornis, Zhou et al., 2008b). This suggests a careful taxonomic review of these poorly preserved specimens was not conducted. Accordingly, the taxonomy of C. aberransis and C. caudatus is revisited here. The taxonomic status of these taxa is discussed individually and with caution; the specimens were not accessed first hand so their validity and anatomy is evaluated from published data. However, we argue that this should be adequate: if published data are not sufficient to differentiate a new species from known taxa, then it does not add to our knowledge of the clade, or facilitate future research; a specimen affixed to a name in this way, although unique, still represents a nomen dubium.

Cathayornis aberransis. Known from a single specimen, IVPP V12353 (Fig. 7A), C. aberransis comes from the Jiufotang Formation of northeastern China (Hou et al., 2002); the specimen was studied from published photos of the slab and counterslab (Hou et al., 2002; Hou, 2003). This taxon was diagnosed by the presence of a crest between the two frontals with processes on the frontal sides (tubercles), numerous teeth in the maxilla, a distally developed sternal carina, sternal outer trabeculae distally ending proximal to the distal end of the xiphoid process ("sternum lateral process no longer than posterior process"), a humerus that is shorter than the ulna, and a distally fused pubis (Hou et al., 2002). Most of these diagnostic characters are weak because they are widely distributed amongst Mesozoic birds, while some (humerus shorter than ulna, presence of teeth in the maxilla, a distally contacting pubis) are plesiomorphic to Ornithothoraces (O'Connor et al., 2009). The morphology of the sternum in IVPP V12353 cannot be confirmed and the distal ends of the pubes are clearly non-contacting and thus, while likely joined in a symphysis in life (evident from their expanded distal

ends), the pubes were not fused (*contra* Hou *et al.*, 2002). The frontals are fairly well preserved in dorsal view, whereas typically enantiornithine frontals are preserved in lateral view. A longitudinal ridge appears absent; the frontals are unfused and the slight medial separation of the two bones may have been interpreted as a ridge. The caudolateral corner of the frontals project ventrolaterally, presumably for articulation with the postorbital and squamosal bones (Fig. 7A). Given the dorsal view, this feature may be exaggerated in *C. aberransis*, however because it cannot be readily compared in terms of exact size and shape to other enantiornithines (visible in lateral view in *Pengornis, Rapaxavis*, LP 4450, GMV 2159, DNHM D2567), this process and morphology are accepted as possibly diagnostic characteristics for this taxon.

While there exists published data supporting the validity of this taxon, albeit weakly, much of the published information has also been shown to be inaccurate and thus studies that incorporate this species must be cautious. Further preparation followed by detailed study is required to verify the validity of this specimen.

Cathayornis caudatus. The holotype and only known specimen of C. caudatus, IVPP V10917 (Fig. 7B), also comes from the Jiufotang Formation, Liaoning, China (Hou, 1997, 2003; Hou et al., 2002). The taxon is diagnosed as a small Cathayornis species with a transverse groove between the frontal and parietal, more than three teeth in the dentary, a well-developed sternal carina, an elongate tarsometatarsus more than half the length of the tibiotarsus, and a short bony tail lacking a pygostyle (Hou, 1997). A toothed dentary and sternum with carina are plesiomorphic to Enantiornithes (Chiappe & Walker, 2002); based on the relative lengths of the femur and tibiotarsus, IVPP V10917 is only 2-5% smaller than C. yandica (IVPP V9769), so the new specimen is essentially the same size as other Cathayornis. Given the poor preservation of the hindlimb in the holotype of C. yandica, the length of the tarsometatarsus relative to the tibiotarsus cannot be accurately compared between the two taxa. No transverse groove or comparable structure on the frontal, which is preserved in lateral view, can be identified from photographs. A fully fused pygostyle of typical enantiornithine morphology (appears forked dorsally and to have possessed a laterally projected flange) is clearly visible in one of the slabs (Hou, 1997; Hou et al., 2002; counterslab in Hou, 2003) overlapping the sternum and pelvic elements (Fig. 7B). The free caudal vertebrae illustrated by Hou (1997) are reinterpreted as the proximal portion of the left pubic shaft. Although currently available published data fail to support the validity of this taxon, further preparation and study of IVPP V10917 may identify unique morphologies that support C. caudatus as a valid taxon. Until this time, this taxon is regarded as a nomen dubium.

Cathayornis chabuensis. The holotype of C. chabuensis, BMNHC Ph000110ab, greatly extends the known geographical range of cathayornithiforms (Zhou & Zhang, 2006); the specimen comes from exposures of the Jingchuan Formation at the Chabu Sumu locality near Otog Banner, in the northwest of the Otog basin, Inner Mongolia, China (Li et al., 2008). The specimen is assigned to Cathayornis on the basis of a longitudinal groove on the dorsal surface of the radius, a narrow intermetacarpal space, and a minor digit formed by single phalanx that closely abuts the first phalanx of the major digit (Li et al., 2008). This suite of morphologies does not diagnose Cathayornis or even distinguish it from other enantiornithines and thus this taxonomic assignment is

unsubstantiated. The presence of a longitudinal groove on the radius is a synapomorphy of a subclade of enantiornithines (Chiappe & Walker, 2002). Most enantiornithines have a minor digit formed by two phalanges, both of which are reduced, the second often to a very small fragment less than 10% the size of the first phalanx (e.g., *Eoalulavis lacustris*, *Longipteryx, Rapaxavis*; Sanz *et al.*, 1996); a second phalanx was likely present in BMNHC Ph000110ab, but may not have been preserved given the disarticulated and incomplete nature of the specimen and the very small size of this phalanx.

The specimen is distinguished from C. yandica by the slightly greater lateral projection of the outer (lateral) sternal trabeculae, as well as the relatively more caudal extension of the keel (Li et al., 2008). Although the quality of published photographs and illustrations makes it difficult to verify these anatomical details given that the keel is not visible and the very minimal degree of lateral splay of the outer sternal trabeculae that is being compared, the specimen was available for study and these differences have been verified. The more caudal extension of the keel, however, is here interpreted to refer to the caudal extension of the xiphial region (xiphoid process) relative to the outer sternal trabeculae; the outer trabeculae end proximal to the caudal xiphial margin (as in Elsornis keni, Shanweiniao cooperorum; Chiappe et al., 2006; O'Connor et al., 2009), as opposed to some enantiornithines in which the two processes end at approximately the same level (e.g., Longipteryx, Protopteryx fengningensis; Zhang & Zhou, 2000) or the outer trabeculae extend beyond the xiphoid process (e.g., Concornis, Rapaxavis). Another apparent distinction between the two species, a well-developed distal expansion appears absent from the outer sternal trabeculae, whereas C. yandica has large asymmetrical fan shaped expansions (also present in *C. caudatus*). The new specimen is further distinguished from previously identified specimens of Cathayornis by its locality, which is over 1000 km away from Chaoyang, Liaoning, where other Cathayornis specimens have been collected. Although this specimen is considered distinct from C. yandica, the characters used to assign this specimen to the cathayornithiforms are unsupported. With limited preserved material for comparison in the holotype of C. chabuensis, the taxonomic assignment of this species may have to await additional discoveries or a better understanding of Cathayornithiformes.

#### Discussion

Here we have provided a comprehensive overview of the taxonomic issues regarding Cathayornis yandica and Sinornis santensis, as well as the less prominent issues of specimens and species assigned to the former. The latter issues may not be as apparent in the literature and thus to the international scientific community, but they represent problems that extrapolate outwards from a single taxonomic issue into many. Taxonomic research, although seemingly mundane, is of great significance and importance to the scientific community. Without sound taxonomy, the results of research can be obscured by synonymous taxa and misidentified specimens. Without rapid rectification of old problems, new taxonomic issues will arise and spread throughout the literature. Taxonomic consistency and accuracy provides a sound base for future research within an international community, facilitating common understanding and cooperative research. While old taxonomy will inevitably require revision, as seen with C. yandica and S. santensis, some revisions do not necessarily clarify issues or produce consistency. The aim of this review was not only to try to resolve this issue and increase future taxonomic consistency between Mesozoic bird researchers, but also to address the reasons why such taxonomic revisions are often necessary.

Vertebrate paleontology is a science that will always be plagued with doubts, assumptions, and missing data. Our knowledge of taxa and their morphology is limited by available fossil material, compromised by the processes of death, fossilization, and diagenesis. It has long been understood that the naming of vertebrate fossil taxa is especially subjective because diagnostic characteristics can be based only on preserved morphology, which can be interpreted differently among workers (Amadon, 1963; Cracraft & Eldredge, 1979): one person examining a fossil may view it as 'considerably different' in morphology compared to someone else. The proliferation of potential synonyms, homonyms and nomina dubia has been especially evident in the study of Mesozoic birds as recent years have seen an explosion in the numbers of known fossils leading to an exponential rise in the number of named taxa since the mid-1990s (Fountaine et al., 2005; Chiappe & Dyke, 2007). While the need for taxonomic revision is not unique to the enantiornithine clade, nor can it ever be avoided entirely, it is observed that in this clade, a majority of these problems arise as a result of (1) the use of inadequate, fragmentary and undiagnostic holotype material (resulting in nomina dubia—taxa that cannot be distinguished from others, e.g., C. caudatus); (2) inadequate comparisons of new taxa with those already described (resulting in the subsequent erection of junior synonyms); (3) differences in interpretation of fossils (perhaps based on observed morphological differences or via a taphonomic effect); and (4) variation in species definitions (basing a new taxon on the fact that it comes from a different locality to other similar forms).

The well-known Chinese fossil enantiornithine birds Cathayornis yandica and Sinornis santensis are both represented by fairly complete specimens yet there has been debate over their status as distinct taxonomic entities. Largely this debate has occurred because clear diagnostic characters had not been presented in the original descriptions, which appeared simultaneously, preventing comparison. However later publications continued to differ on this matter as a result of differential interpretation of preserved morphologies and their significance. Close inspection reveals important morphological differences indicating that these two taxa are clearly distinct from one another and should remain separate taxa. Assigned species of Cathayornis remain ambiguous from published data, suggesting that the ability to differentiate and diagnose IVPP V9769 and BNHM BPV 538 may be in large part due to their preparation. In these specimens, bones were removed to create clean voids and moulds and casts were made for study so that the maximum amount of data could be retrieved from each specimen. Despite the fact new species were erected from these specimens, preparation is largely absent in the holotypes of C. caudatus and C. aberransis, making it difficult to clearly establish morphological differences. Casts were made of BMNHC Ph000110ab, and C. chabuensis can be distinguished from other known taxa (Li et al., 2008).

While disagreements about taxonomic validity and the interpretation of a given morphology result in new ideas and stimulates research, the erection of taxa based on fragmentary materials without a clear diagnosis serves only to slow the progress of research into a given clade. Despite the system of peer review and its intended purpose, large numbers of taxa

of fossil birds have been described with inadequate diagnoses (Hou, 1997; Li et al., 2006). When a taxon lacks an accurate diagnosis, the validity of the taxon is questioned making the species a potential nomen dubum. With the global distribution of Enantiornithes in mind, individual access to every specimen is unlikely and thus publications must include important and pertinent data so that there is no question regarding the species validity. In the case of C. aberransis and C. caudatus, the morphological features cited in the published diagnoses for these species could nearly all either be invalidated from the photographic data or are not diagnostic features (plesiomorphies). Furthermore, preservation and the quality of preparation and published photographs prevent independent detailed morphological inspection and the identification of autapomorphies. Because the publications are uninformative, these taxa become functional nomina dubia.

Others species have been described based on specimens in private collections, unavailable to the scientific community, and thus rendering any interesting data they may have to contribute unverifiable and useless (*Dalingheornis liwei*; Zhang *et al.*, 2006). The most recent example of this worrying trend is the description of a new, small enantiornithine bird from the Crato Formation of Brazil (Naish *et al.*, 2007), potentially the oldest fossil bird known from Gondwana (Close *et al.*, 2009), but held in a private colletion.

The biggest problem of all, however, is the erection of taxa based on largely incomplete specimens (Table 1; e.g., Explorornis nessovi, Lectavis bretincola, Martinavis cruzyensis; Panteyelev, 1998; Chiappe, 1993; Walker et al., 2007). Over a third of all known enantiornithines are named from bone fragments (less than a single whole bone); these specimens may be interesting to the scientific community because they extend a temporal or geographic range, but their existence as distinct taxa is unjustifiable given the inability to compare the specimens to a majority of known taxa and specimens. For whatever reason scientists are compelled to erect taxa from fragmentary material, it is up to the scientific community as reviewers to prevent undiagnosible or comparable specimens from being named. When taxa are based on private material, or are for other reasons invalid, the scientific community should unify in excluding these 'taxa' when discussing the clade they are purported to belong to. This will hopefully discourage the continued practice of the erection of such taxa (e.g., Dalingheornis, Zhang et al., 2006). While it is very important to describe new material, erecting a new genus based on a bone fragment or publishing information that can never be verified does little to help clarify enantiornithine diversity and relationships.

#### **Conclusions**

Differences will always exist in preferred taxonomic requirements; differences in opinion lead to new investigations, and ultimately greater knowledge. However if a proposed new taxon serves only to increase ambiguity within the taxonomy of a clade, then we urge editors and reviewers to reject such research. The peer review system is in place to ensure that published data maintains a certain level of quality. This is to protect the integrity of published data and facilitate future research. Species based on highly fragmentary material, unprepared materials, or private collections should be rejected. Any publication that does not adequately document a new taxon should be subject to revision so that additional publications on the morphology of a single specimen are not required. In the cases of *Cathayornis yandica* and *Sinornis* 

santensis, the original publications appeared simultaneously preventing comparison at the time and the similarity of the species necessitated further review. In the cases of *C. aberransis* and *C. caudatus*, the original publications fail to provide valid arguments for the erection of new species, and have thus made revisionary research absolutely necessary. After reviewing these issues, the morphological differences between the holotypes of *Cathayornis yandica* and *Sinornis santensis*, some already noted by Sereno *et al.* (2002) and Zhou & Hou (2002), are utilized to distinguish the two taxa. Because of similarities between these taxa, future identifications of morphologically comparable specimens require detailed study to prevent the need for further revision.

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